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Beyond EICA: understanding post-establishment evolution requires a broader evaluation of potential selection pressures

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Abstract

Research on post-establishment evolution in nonnative plant populations has focused almost exclusively on testing the Evolution of Increased Competitive Ability (EICA) hypothesis, which posits that the lack of specialized herbivores in the invaded range drives evolution in nonnative plant populations. Fifteen years of conflicting EICA test results suggest that selection pressures other than specialized herbivory are important in driving post-establishment evolution in invasive species. Alternative hypotheses, such as the Evolution of Reduced Competitive Ability (ERCA) hypothesis, have been proposed but have received little attention or testing. We argue that the lack of consensus across studies that test EICA may be due in part to the lack of consistent definitions and varying experimental design parameters, and that future research in this field would benefit from new methodological considerations. We examined previous work evaluating post-establishment evolution and evaluated the range of study systems and design parameters used in testing the EICA hypothesis. Our goal was to identify where different uses of ecological terms and different study parameters have hindered consensus and to suggest a path forward to move beyond EICA in post-establishment evolution studies. We incorporated these methods into a design framework that will increase data harmony across future studies and will facilitate examinations of any potential selection pressure driving evolution in the invaded range.

Keywords

EICA, ERCA, invasion ecology, invasive plants, natural selection

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Introduction

It has been commonly observed that life-history traits of nonnative plant species vary across habitats in native and introduced ranges, most conspicuously as either increased growth (Crawley 1987; Thebaud and Simberloff 2001) or decreased growth (Crawley 1987; Siemann and Rogers 2003a; Bossdorf et al. 2004). While trait variations across habitats may in some cases be plastic (i.e., non-genetic) responses to local environmental conditions (e.g., Fowler et al. 1996; Willis et al. 2000; Keane and Crawley 2002), a growing number of studies have examined this variation from an evolutionary perspective: the characteristics of the invaded habitat amount to a suite of novel selection pressures that drive post-establishment evolution in invading populations (e.g., Blossey and Nötzold 1995; Cody and Overton 1996; Table 1). To date research regarding post-establishment evolution has been heavily focused on testing the Evolution of Increased Competitive Ability (EICA) hypothesis. This hypothesis posits that nonnative plant populations may evolve a modified energetic tradeoff in which vegetative growth is increased while herbivore defense is decreased due to the lack of specialized herbivores in the invaded range. The potential for increased reproductive effort was also discussed, though not tested (Blossey and Nötzold 1995). Increases in vegetative growth were interpreted broadly by Blossey and Nötzold (1995) as "increased competitive ability."

Because research regarding post-establishment evolution has been so tightly focused on testing the EICA hypothesis, much of the literature in this field evaluates a single reduced selection pressure: the lack of specialized herbivores in the invaded range. However, the inconclusive support found for the EICA hypothesis suggests that factors other than herbivore release may drive post-establishment evolution in some systems (Bossdorf et al. 2005; Fornoni 2010). To this end, researchers have called for an expanded consideration of habitat characteristics that may act as selection pressures in the invaded range (Callaway and Maron 2006; Whitney and Gabler 2008). As this field expands, however, the approaches to testing hypotheses focused on post-establishment evolution merit careful consideration so that results across studies can be more easily used to form generalized conclusions. In addition, transitioning the focus from "competitive ability" (which is not well defined in this context) would enhance future research by more broadly focusing on evolved trait modifications that impact survival and fecundity.

There have been a handful of studies evaluating selection pressures other than specialized herbivory, although they have not received the attention and scrutiny given to the EICA hypothesis. Maron et al. (2004), for example, demonstrated morphological adaptations associated with latitude in nonnative populations of *Hypericum perforatum*, and Van Grunsven et al. (2009) found that a lack of soil pathogens resulted in increased growth for nonnative populations of *Carpobrotus edulis*. More broadly, Bossdorf et al. (2004) proposed the Evolution of Reduced Competitive Ability (ERCA) hypothesis, which posits that post-establishment evolution can be driven by the amount of plant competition found in the invaded habitat. Specifically, plant populations invading areas with fewer competitors should evolve an energetic tradeoff in which vegetative growth is decreased while other traits such as reproductive effort or herbivore defense

Table 1. Published hypotheses related to post-establishment evolution.

Reference	Description
Blossey and Nötzold 1995	*Evolution of Increased Competitive Ability (EICA):* Evolved increase in growth, decrease in defense associated with lack of herbivores in invaded range.
Sexton et al. 2002	Invading populations benefit first from plasticity, then from local adaptation
Maron et al. 2004	Latitudinal clines drive local adaptations in nonnative populations.
Bossdorf et al. 2004	*Evolution of Reduced Competitive Ability (ERCA):* Low amounts of plant competition result in an evolved decrease in growth, increase in reproduction, and defense.
Roman 2006	Multiple introductions and hybridization increase invasion success through increased genetic variability.
Blumenthal 2006	*Resource-Enemy Release Hypothesis (R-ERH):* Resource availability effects how enemy release drives plastic and genetic trait variation.
Van Grunsven et al. 2009	The absence of soil pathogens results in an evolved increase in growth.

are increased (Bossdorf et al. 2004). One potential implication of this hypothesis is that intraspecific competitive interactions may be reduced in monotypic or near-monotypic stands, increasing stand-level fitness while decreasing individual growth. A test of this hypothesis in any organism or geographic system has not yet been published.

Expanding our knowledge of post-establishment evolution beyond evaluations of the EICA hypothesis would address the omission of evolutionary potential from invasive species weed risk assessments, which attempt to predict the impact of an invading species on a given habitat based on the combination of species traits and habitat characteristics (Whitney and Gabler 2008). A better understanding of how the traits of invading species may rapidly change over time via natural selection would facilitate predictions regarding the immediate and long-term impacts of a given invasion (Daehler et al. 2004; Whitney and Gabler 2008). Such an understanding requires evaluations of not only those selection pressures posited by EICA or ERCA, but any number of habitat characteristics that vary across the native and invaded ranges of a given species.

We examined previous work regarding post-establishment evolution in order to better understand why outcomes across studies have been inconsistent. Because this literature has focused primarily on testing the EICA hypothesis, we focused our analysis within the field of evolution and invasive species by specifically examining tests of the EICA. Unlike previous reviews, we specifically evaluated study systems and methodologies in order to identify design parameters that will allow better synthesis across research on post-establishment evolution. We also focused on the use of the term "competitive ability" and how its definition varied based on the context of experimental designs. We searched for relevant literature published since the introduction of EICA that explicitly tested the predictions of the EICA hypothesis in a common garden or reciprocal transplant design, resulting in 58 studies. We focused on common garden and reciprocal transplant designs because of their frequent use and their ability to minimize the effects of phenotypic plasticity in the examination of evolved trait differentiation. We reviewed each study and

recorded information regarding study systems and design parameters, including whether abiotic and biotic variables were reported for seed collection sites, the inclusion of introduction history, sample size, the traits measured and metrics used, and the incorporation (or lack thereof) of competition in experimental manipulations. We also noted whether each study ultimately found support for the predictions of the EICA hypothesis (Table 2).

Based on our results, we developed a framework that can be used to move beyond EICA to evaluate a broad range of habitat characteristics that can act as selection pressures driving post-establishment evolution. Our intent is to facilitate future research that expands the consideration of potential selection pressures and encourages integration of results across study species and organisms.

Methodological variability in evaluating selection pressures: lessons from tests of the EICA hypothesis

The variation in sample sizes of both native and nonnative populations used in common garden research is one of the most readily apparent differences among studies of post-establishment evolution (Table 2). The logistical difficulties of obtaining individuals from both the introduced and invaded ranges likely contribute to the small number of populations used to represent each range in most studies. Though a handful of studies used ten or more populations in each range (e.g., Blossey 1996; Blair and Wolfe 2004; Güsewell et al. 2006), most tests of the EICA hypothesis have used a small number of populations (e.g., <10) and 13 of the 58 studies we reviewed used just one population to represent a native or invaded range (e.g., Blossey and Nötzold 1995; Lankau et al. 2004; Rogers and Siemann 2005; Franks et al. 2008).

Most of the studies we examined measured only one trait despite the fact that hypotheses focused on post-establishment evolution generally discuss multiple traits related to one another through energetic tradeoffs. The EICA hypothesis makes two predictions that were explicitly tested by Blossey and Nötzold (1995): that nonnative populations will demonstrate increased growth and will also demonstrate decreased herbivore defense. Of the 58 studies we reviewed, only 15 examined differences in both growth and defense in the same species. Of these, only eight found support for both predictions of the EICA hypothesis (Table 2). Twelve of the 58 studies identified reproductive effort as a third energetic "sink" in evolved tradeoffs, though only three studies quantified all three of these traits in the same species (Fig. 1, Table 2).

Common garden designs also varied by study, either as outdoor gardens or greenhouse benches. Those studies that used outdoor gardens diverged further in whether plants were grown in pots (e.g., Willis and Blossey 1999) or were planted directly into the ground (e.g., Siemann and Rogers 2001). Each approach has its advantages and disadvantages: while greenhouse studies allow researchers to better control environmental variables such as temperature or photoperiod, some researchers have argued that growth under these conditions may be too artificial for evaluating growth in wild populations (Gibson et al. 1999).

Table 2. Design parameters of studies testing the EICA hypothesis. In the column labeled "Abiotic data," "1" indicates that researchers tried to incorporate a variety of abiotic environments in seed collection sites while "2" indicates that researchers tried to utilize similar environments. In the column "Traits," "G" = vegetative growth, "T" = herbivore tolerance, and "R" = reproductive effort. The column labeled "Comp." indicates whether or not competition was incorporated into experimental manipulations. For "Metrics," growth metrics are denoted by "B" = biomass, "H" = height, "NL" = number of leaves, " "LA" = leaf area, "BA" = basal area; tolerance metrics are denoted by "HM" = herbivore mass, "HA" = herbivore abundance, "LD" = leaf damage, "DC" = defense chemicals, "TD" = trichome density; reproductive metrics are denoted by "RM" = reproductive mass, "ReMR" = reproductive mass ratio, and "NF" = number of fruits. In the column "Sample Size," the values correspond to the number of native and nonnative populations used, respectively, unless the sample size was not differentiated by range. The column "EICA" indicates whether support was found, with "Partial" indicating that multiple traits were tested but not all results supported predictions, and "1" indicating that support was found, but only when plants were grown in the absence of competition.

Article	Abiotic data	Intro. Hist	Traits	Comp.	Metrics	Sample size	EICA
Abhilasha and Joshi 2009	No	Yes	G T R	No	B, HA, RM	8&22	Yes
Bastlová and Kvet 2002	Yes	No	G	No	B, ReMR	3&3	Yes
Blair and Wolfe 2004	No[1]	No	G T R	Yes	NL, TD, RM	20&20	Yes
Blossey 1996	No	Yes	G T	No	B, HA	13&23	Yes
Blossey and Nötzold 1995	No	Yes	G T	No	B, H, HM	1&1	Yes
Blumenthal and Hufbauer 2007	No[2]	No	G	Yes	B	2&2	Yes[1]
Bossdorf et al. 2004	Yes[2]	Yes	G R	Yes	H, B, RM	8&8	No
Bossdorf et al. 2008	Yes	Yes	G R	No	B, NF	11&12	No
Brown and Eckert 2005	No	Yes	R	No	RM	6&5	Yes
Buschmann et al. 2005	Yes[2]	Yes	G T R	No	B, NL, NF	1&1	Partial
Cano et al. 2008	Yes[1]	Yes	G	No	LA	4&4	Yes
Cano et al. 2009	No	Yes	G T	No	B, LA	3&3	No
Cipollini et al. 2005	No	Yes	T	No	DC	4&7	No
Cripps et al. 2009	Yes[1]	Yes	G	No	B, HA	6&10	No
Daehler and Strong 1997	No	Yes	R	No	RM	4&1	Yes
DeWalt et al. 2004	Yes	Yes	G	No	B	4&4	No
Eigenbrode et al. 2008	No	Yes	T	No	DC	4&3	No
Erfmeier and Breulheide 2005	Yes[2]	Yes	G	No	H	6&6	Yes
Franks et al. 2008	No	Yes	G T	No	B, HA	1&1	No
Genton et al. 2005	No	Yes	G T	No	B, LD	2&1	No
Güsewell et al. 2006	No	No	G	No	B, NL	20&22	Yes
Handley et al. 2008	No	Yes	T	No	LD	8&16	No
He et al. 2009	No	No	G	Yes	B	8&9	No
Henery et al. 2010	No	Yes	G	No	B	45	No
Herrera et al. 2011	No	Yes	T	No	HM	3&3	No
Huang et al. 2010	No	Yes	T	No	HM	6&6	Yes
Hull-Sanders et al. 2007	No	Yes	T	No	HM, DC	10&20	No
Johnson et al. 2007	No	Yes	T	No	DC	10&22	Yes
Joshi and Vrieling 2005	No	Yes	T	No	DC, HM	13&16	Partial
Lambert and Casagrande 2007	No	No	T	No	HA	6&4	No

Article	Abiotic data	Intro. Hist	Traits	Comp.	Metrics	Sample size	EICA
Lankau et al. 2004	No	Yes	G T	No	B, LD	1&1	No
Leger and Forister 2005	No[1]	Yes	T	No	HM	7&4	No
Leger and Rice 2003	Yes[2]	Yes	G	Yes	B	10&10	Yes[1]
Lym and Carlson 2002	No	No	R	No	HA	1&6	No
Maron et al. 2004	No	Yes	G R	No	B, NF	18&32	No
McKenney et al. 2007	Yes	Yes	G	Yes	B	10&10	No
Meyer and Hull-Sanders 2008	No	Yes	G R	No	H, LA, ReMR	10&20	No
Meyer et al. 2005	No[1]	Yes	G T	No	H, HM	10&20	Partial
Müller and Martens 2005	Yes	Yes	G T	No	B, DC	11&10	No
Ridenour et al. 2008	No	No	G R	Yes	B, NF	22&23	Partial
Rogers and Siemann 2004	No	No	G	Yes	B	1&1	Yes
Rogers and Siemann 2005	No	Yes	T	No	HM	1&1	Yes
Rogers et al. 2003	No	No	T	No	NL	1&1	No
Siemann and Rogers 2001	No[1]	Yes	G T	No	BA, DC	1&1	Yes
Siemann and Rogers 2003a	No	Yes	G T	No	BA, LD, DC	1&1	Yes
Siemann and Rogers 2003b	No	Yes	G T	No	H, LD, HM	1&1	Yes
Stastny et al. 2005	Yes	No	G T	No	LA, DC	4&4	Partial
van Kleunen and Fischer 2008	Yes[2]	Yes	G R	No	# Branches, Flowers	17&7	Yes
van Kleunen and Schmid 2003	No	Yes	T	No	H	9&10	No
Vilà and Gimeno 2005	Yes	Yes	R	No	NF	30&20	Yes
Vilà et al. 2003	No[1]	Yes	G	Yes	B	10&20	No
Widmer et al. 2007	No	Yes	G	No	H	7&8	Yes
Williams et al. 2008	Yes	Yes	G	No	Plant volume	10&10	No
Willis et al. 1999	No	No	G	No	B, H	10&10	Yes
Willis et al. 2000	No[1]	No	G	No	B	3&3	No
Zou et al. 2007	No	No	G	No	B, H	4&4	Yes
Zou, Rogers, and Siemann 2008	No	Yes	T	No	B, LD	9&9	Yes
Zou et al. 2008	No	Yes	G T	Yes	B, LD	2&2	Yes

The term "competitive ability" had multiple interpretations across the studies that we reviewed. In studies where individuals are grown alone (e.g., Blossey and Nötzold 1995; Maron et al. 2004), "competitive ability" appeared to be interpreted as the ability of an individual to secure resources for itself regardless of the presence of neighbors. Alternatively, studies in which individuals are grown alongside competitors (e.g., Leger and Rice 2003; Vilà et al. 2003; Bossdorf et al. 2004) appeared to interpret "competitive ability" as the ability of an individual to preempt resources for itself specifically in the presence of neighbors. The distinction is an important one: Blumenthal and Hufbauer (2007) found that biomass was higher in nonnative populations than native populations when grown in a common garden, but only when individuals were grown alone. When exposed to actual competition, there was no difference in biomass between nonnative and native populations. Of the 58 studies we examined, only

ten exposed individuals to actual competition by growing study individuals alongside competing neighbors. Of these, only one found support for both predictions of the EICA hypothesis (Fig. 1, Table 2).

These different definitions of competitive ability have also muddled our understanding of the energetic tradeoffs being examined in these studies. The focus on testing EICA has resulted in the general adoption of the term "competitive ability" as synonymous with "vegetative growth," as it was interpreted by Blossey and Nötzold (1995). This is an oversimplification since EICA links multiple traits that are influenced by competition through energetic tradeoffs, including growth, defense, and, in more recent work, reproduction (Herms and Mattson 1992; Bazzaz and Grace 1997; Table 2). It is possible that, as predicted by the ERCA hypothesis, nonnative plant populations could produce decreased total biomass but increased fruit mass, resulting in increased fecundity in future generations (Bossdorf et al. 2004). This would be considered reduced competitive ability despite the increased success of the nonnative plant population.

The use of different metrics for quantifying plant traits presents further challenges for data comparison across studies. While Blossey and Nötzold (1995) utilized biomass and height as growth metrics, subsequent tests of EICA have used a wide variety of alternative metrics including plant volume (e.g., Maron et al. 2004), basal area (e.g., Siemann and Rogers 2003a), leaf area (e.g., Blair and Wolfe 2004), number of branches (e.g., van Kleunen and Fischer 2008), and leaf length (e.g., Stastny et al. 2005) (Table 2, 3). Similarly, the measurement of plant responses to herbivory has varied among studies and includes herbivore larval mass (e.g., Blossey and Nötzold 1995; Willis et al. 1999; Joshi and Vrieling 2005; Hull-Sanders et al. 2007), leaf damage (e.g., Buschmann et al. 2005; Genton et al. 2005), the number of herbivores present (e.g., Meyer et al. 2005; Franks et al. 2008), or concentrations of chemical defense compounds such as alkaloids, terpenes, and phenolics (e.g., Willis et al. 1999; Siemann and Rogers 2003a; Cipollini et al. 2005; Joshi and Vrieling 2005; Johnson et al. 2007) (Table 2, 3).

In evaluating specialized herbivory as a selection pressure, studies of post-establishment evolution have generally neglected other habitat characteristics that can act as confounding variables across seed collection sites. Because comparisons of native and nonnative populations often use seeds collected on different continents, abiotic characteristics such as photoperiod or climate may vary significantly across the study area. For example, of the 58 studies we reviewed, only 15 identified differences in abiotic conditions (e.g., climate and/or photoperiod) between the native and invaded ranges. None of the studies we reviewed recorded information regarding the biotic characteristics of the collection site (e.g., plant community composition) other than differences in herbivore assemblages (Fig. 1, Table 2). This is particularly significant in light of a study by Williams et al. (2008), which found that the results of common garden experiments change depending on the geographic location and habitat characteristics of the common garden.

Furthermore, the 15 studies that did report abiotic characteristics often disagreed as to whether consistency in abiotic factors across the sampling range was a desired

Table 3. The metrics used to quantify growth, herbivore tolerance and reproduction in studies examining post-establishment evolution. Data are aggregated from our review of design parameters detailed in Table 2.

Trait	Metric
Growth	Total biomass
	Aboveground biomass
	Belowground biomass
	Height
	Plant volume
	Basal area
	Leaf area
Reproduction	Number of flowers
	Fruit mass
Herbivore Tolerance	Herbivore mass
	Number of herbivores
	Defense chemical concentration
	Leaf damage

component of the experimental design, despite having similar aims in evaluating evolution in nonnative populations. Several studies noted that seeds utilized in a common garden were intentionally collected from a wide variety of habitat types in order to incorporate environmental heterogeneity across the distribution of the species (e.g., Siemann and Rogers 2001; Vilà et al. 2003; Cano et al. 2008; Cripps et al. 2009). Cripps et al. (2009), for example, chose populations "covering a wide geographic range to obtain representative samples" across the distribution of *Lepidium draba*. Conversely, other studies noted that seeds for common gardens were collected from very similar habitats in order to minimize the potential for confounding habitat variables (e.g., Leger and Rice 2003; Buschmann et al. 2005; Blumenthal and Hufbauer 2007). Erfmeier and Bruelheide (2005), collected seeds only from populations of *Rhododendron ponticum* growing on north-facing, forested slopes with an aspect of 10–20°. This variation in experimental design demonstrates a fundamental difference in how researchers assess the potential for confounding variables and leads to varying degrees of robustness across studies.

Introduction history and subsequent spread of an invader are potentially influential factors often missing in reports of post-establishment evolution. This history is fundamental to understanding the selection pressures to which a species has been exposed. For example, Maron et al. (2004) used genetic analyses to determine that multiple introductions of *Hypericum perforatum* had occurred in the US, thereby influencing the amount of genetic variability in nonnative populations. However, detailed introduction histories are often unavailable and genetic analyses can be time- and cost-intensive, likely contributing to the omission of such information from many studies. Of the 58 studies we examined, 44 studies reported some data regarding introduction history, though often this information was limited to the date of first introduction to a country or continent and as such does not provide a detailed description. The remain-

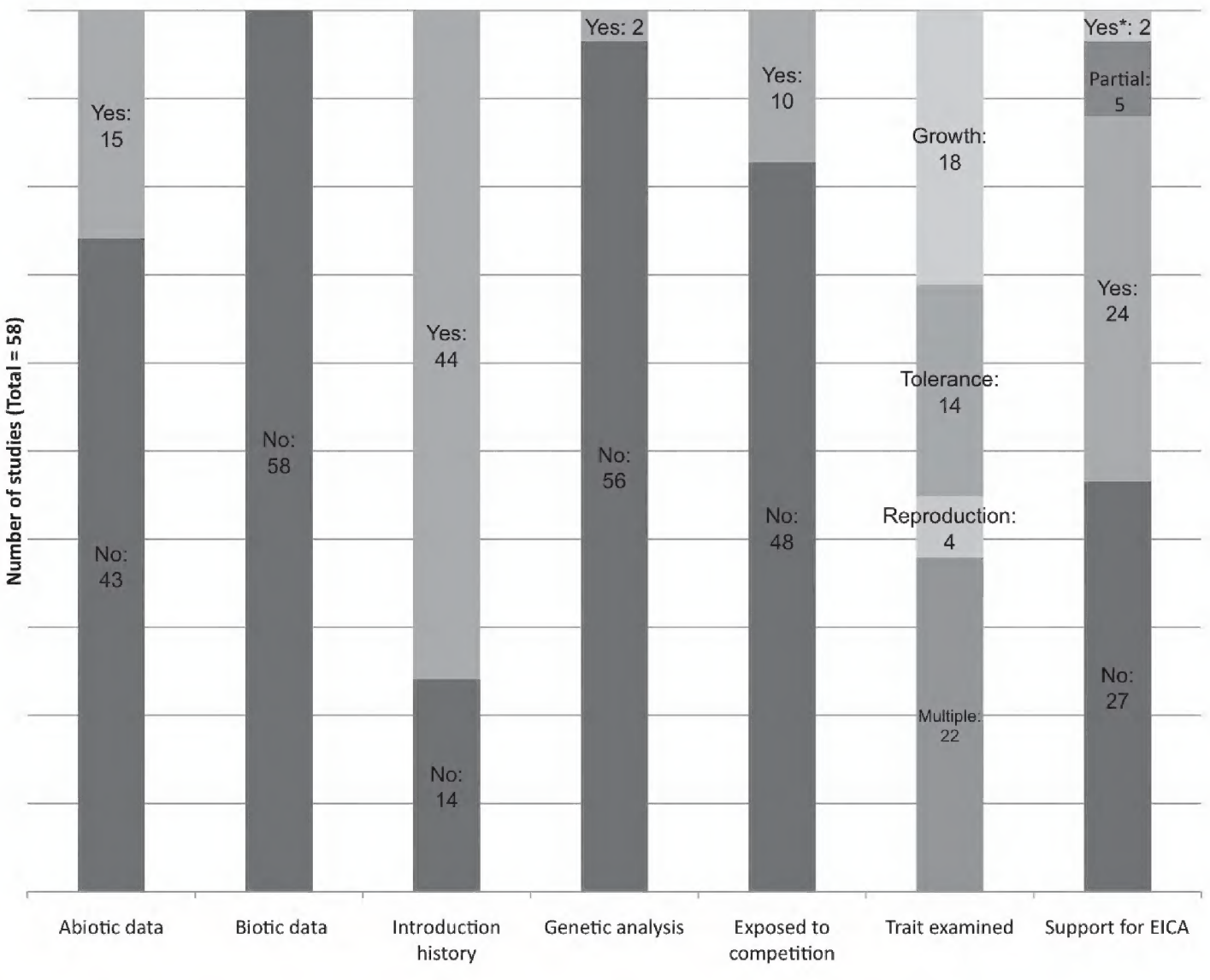

Figure 1. Frequencies of methodologies used in EICA studies. Data are aggregated from our review of design parameters detailed in Table 2. "*" Indicates that support for the EICA hypothesis was found only when plants were grown in the absence of competition.

ing 14 studies made no mention of introduction history. Only two studies conducted genetic analyses to assess variability among populations (Fig. 1, Table 2).

The broad range of approaches used in testing EICA may be one factor that limits its consensus among the collective results. Twenty-four of the 58 studies we examined found support for the predictions of the EICA hypothesis, while 27 did not. Five studies found partial support, and two found support only when individuals were not exposed to competition (Fig. 1, Table 2). While EICA is likely an accurate predictor of evolutionary changes in some (but not all) of the species on which it has been tested, the fundamental differences in experimental designs and the use of loosely defined terms such as "competitive ability" in these studies may have hindered a more complete understanding of the applicability of the EICA hypothesis and of post-establishment evolution in general. While it is possible that meta-analyses could be used to make generalizations across methodologies (e.g., Colautti et al. 2009), the ecological relevance of results might be easier to interpret if some fundamental design parameters, such as the incorporation of competition into experimental manipulations, were similar across studies.

Post-establishment evolution is an area of research that has attracted substantial attention since the introduction of the EICA hypothesis, but the tests to date have not

yet provided a meaningful consensus. One approach to facilitate progress in this field is to move towards standard definitions and comparable approaches that will more specifically evaluate potential selection pressures beyond the predictions of the EICA hypothesis.

Moving forward: A framework for designing evaluations of selection pressures in post-establishment evolution

Based on our analysis, we developed a framework for future research on selection pressures potentially driving evolution. We focused our recommendations on experimental designs that reduce the potential for confounding factors and increase the ability to integrate results among studies (Table 4).

1. Consider abiotic and biotic conditions across ranges

Studies that examine a potential selection pressure should account for other habitat characteristics that may confound results. Ideally, the study system used for testing a post-establishment evolution hypothesis would use two ranges that are as similar as possible for all factors *except* for the characteristic being evaluated as a potential selection pressure. In particular, researchers can use seed collection sites at similar latitudes to partially control for photoperiod and climate (e.g., Blumenthal and Hufbauer 2007). Whether a study incorporates seed collections from separate continents or uses a smaller study area within a continent, a description of the environmental characteristics across the study system, including plant community composition, would inform comparisons across studies (e.g., Ebeling et al. 2008).

2. Choose study species with appropriate life-history strategies

Study species selected to test post-establishment evolution hypotheses are ideally those that have a high potential for rapid evolution. Species that reproduce primarily by seed rather than clonal growth will have a higher frequency of genetic recombination, as will species with relatively short generation times such as herbaceous perennials. As such, r-selected species may be good candidates for studying post-establishment evolution, though we do not suggest that the role of K-selected species should be ignored. In testing hypotheses related to herbivore damage, it is appropriate to consider the relative effects of specialist and generalist herbivores on a given study species (e.g., Huang et al. 2010). The ability of a species to self-fertilize may also affect the likelihood of adaptive evolution. Species that cannot self-fertilize will have higher outcrossing rates and may accumulate beneficial adaptations more rapidly than self-fertilized species. However,

Table 4. A framework for testing post-establishment evolution hypotheses.

1.	Evaluate the variability in abiotic and biotic conditions across ranges
2.	Choose study species with appropriate life-history traits
3.	Include introduction history
4.	Incorporate competition in manipulations
5.	Measure multiple traits and avoid the term "competitive ability"
6.	Use standard metrics where possible

species that self-fertilize may exhibit stronger founder effects that could accelerate divergence from ancestral populations. Byers and Waller (1999) conducted an in-depth review of the evolutionary advantages and disadvantages of inbreeding, showing that while inbreeding populations tend to rapidly accumulate mutations, inbreeding may increase the likelihood of purging disadvantageous alleles from a population. Species that are known to hybridize with congeners may not be well suited for evolutionary studies, since the introduction of genetic material from other species may introduce novel traits that could mask the influence of selection (Roman 2006).

3. Consider introduction history

Documenting the introduction and historic spread of a given species can reveal the types and durations of selection pressures that the species has undergone. The possibility of multiple introductions should also be considered since repeated introductions can increase genetic variation and/or result in novel genetic admixtures not found in the native range (Maron et al. 2004). Where detailed records of species introduction are unavailable, genetic analyses can potentially determine relatedness of introduced populations. Hufbauer and Sforza (2008), for example, used chloroplast DNA to infer the history of introduction from Eurasia to North America for two species of *Centaurea*.

4. Incorporate competition in manipulations

Because individuals in nature rarely grow in isolation, tests in which individuals are exposed to actual competition are likely to be more ecologically relevant. Incorporation of multiple competitive scenarios in common garden experiments will enhance our understanding of traits that are affected by competition. For example, growing individuals along a gradient of competitive stress (measured as the number of individuals per pot) would provide more information on the ability of a given species to obtain and utilize resources. The ratio of the number of individuals in a pot to soil volume can also be kept constant to avoid confounding competition with density (Gurevitch et al. 1990).

5. Measure multiple traits and avoid the term "competitive ability"

Previous studies related to post-establishment evolution have used the term "competitive ability" as synonymous with vegetative growth, despite discussing growth in the context of energetic tradeoffs with other traits that may be affected by resource competition, including reproductive effort and herbivore tolerance (Blossey and Nötzold 1995; Bossdorf et al. 2004). A strict definition of "competitive ability" is lacking. Grime defined "competition" as the tendency of neighboring plants to use the same resources (Grime 1973), and thus "competitive ability" should be the ability to secure those resources. These resources may then be utilized for a variety of traits related to survival and fecundity, including (but not limited to) growth, reproduction, and herbivore tolerance, but the use of any one of these traits as being synonymous with "competitive ability" would be misleading. Future research could quantify variation in a broader suite of traits and refer more generally to survival and fecundity rather than using the loosely defined term "competitive ability."

6. Use standard metrics where possible.

The variety of metrics used to measure growth, reproduction, and herbivore defense has made it difficult to integrate data across studies. Utilizing standard metrics or converting units to those of standard metrics could facilitate such comparisons. Vilà and Gimeno (2006), for example, used the number of stems of *Oxalis pes-caprae* as a growth metric, but converted their data to units of biomass using an allometric equation. Total biomass is non-dimensional and removes bias for vertical rather than lateral growth.

In studies measuring reproductive effort, a metric that demonstrates the energetic investment in reproductive biomass relative to total biomass is useful in accounting for the role of plant size in determining the amount of fruit produced. The reproductive mass ratio (ReMR=[fruit mass][total biomass]$^{-1}$) has been used to describe the production of reproductive structures relative to total biomass production (Abrahamson and Gadgil 1973; Bastlová and Kvet 2002; DeWalt et al. 2004).

Compensatory growth response is a good candidate as a standard measure for quantifying the effect of herbivory. While many studies have used quantified defense chemical concentrations, not all plant species utilize the same chemical pathways. As a metric of response to herbivory, compensatory growth is relevant across all species that utilize different chemical pathways and therefore facilitates comparisons across studies. Agrawal et al. (2005) used plant biomass to measure the response to herbivory for native and introduced species of Brassicaceae and found that exposure to herbivory resulted in a significant decrease in biomass production for native plants and no difference in biomass production in introduced plants.

Conclusion

Research on post-establishment evolution offers the potential for a better understanding of how nonnative plant populations interact with and adapt to their host environments. These data are relevant not only to invasion ecology, but also to studies of successional ecology and range expansions, as these fields also deal with new species interactions and novel habitat conditions (Davis et al. 2001; Simmons and Thomas 2004; Mitchell et al. 2006). The focus of previous work in this field on testing the EICA hypothesis has demonstrated that while EICA may describe evolution in some study systems, it does not fully explain the evolutionary response of nonnative plant populations to their invaded habitats. A broader examination of potential selection pressures is required to more fully understand post-establishment evolution. Careful consideration of experimental design parameters should be given to future research in this field. The lessons learned from tests of the EICA hypothesis can be used to guide future research that tests the EICA or ERCA hypotheses, or any other selection pressure that may drive post-establishment evolution.

Understanding how nonnative populations change over time is fundamental to their effective management, particularly with respect to weed risk assessments that attempt to predict the ways in which a given species might interact with a given habitat. Data on the evolutionary response of invading plant species can be used to incorporate evolutionary potential into such predictions, filling a knowledge gap that will allow researchers to predict not only the immediate impact of species invasions, but also how rapid evolutionary changes might over time alter the type or magnitude of those impacts (Whitney and Gabler 2008). Future studies that evaluate additional selection pressures will increase our understanding of how habitat characteristics drive adaptations. This information could be used to create regionally specific weed risk assessments that would prioritize management efforts and more effectively respond to current and potential threats (Daehler et al. 2004; Whitney and Gabler 2008). This enhanced understanding of how certain habitat characteristics drive rapid evolution will become increasingly relevant as trade, development, and global change alter habitat characteristics around the world.

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